Effect of spawning time on egg quality, larval morphometrics and survival of Northern pike *Esox lucius*

by

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Abstract. – This study deals with the evaluation of egg and larval qualities for the Northern pike *Esox lucius* Linnaeus, 1758 according to two dates during a spawning season, on March 16 (ST1) and 23 (ST2). A higher hatching rate (97% for ST1 *vs* 80% for ST2) associated to a stronger resistance to starvation (21.0 days for ST1 *vs* 19.1 days for ST2) and a better survival rate (72% for ST1 *vs* 59% for ST2) were found to characterize larvae hatched from eggs spawned earlier. Moreover, a significant female effect was observed for the egg weight, the fertilization rate, the initial total length, the final weight and the resistance to starvation, where some homogeneities were found between eggs and offspring of different females from the two spawning times. Our results suggest the existence of an early organization of pike larval quality, which gives rise to two groups of larvae with different characteristics. Late season individuals were of a large size and a fast growth while early season ones were smaller but survived longer and resisted better to unsuitable feeding conditions. This particularity is likely to be related to a special metabolic ability allowing pike larvae hatched earlier on the spring season to decrease energetic costs in order to survive longer in the absence of adequate food.

Résumé. – Effet du moment de ponte sur la qualité des œufs, la morphométrie et la survie des larves du brochet *Esox lucius*.

Cette étude a porté sur l'évaluation de la qualité des œufs et des larves chez le brochet *Esox lucius* Linnaeus, 1758 en fonction de deux moments de pontes durant une saison de ponte : le 16 mars (MP1) et le 23 mars (MP2). De meilleurs taux d'éclosion des larves (97 % pour MP1 *vs* 80% pour MP2) associés à une résistance accrue au jeûne (21,0 jours pour MP1 *vs* 19,1 jours pour MP2) et à un meilleur taux de survie (72% pour MP1 *vs* 59% pour MP2) ont caractérisé les larves de brochet issues d'œufs pondus en début de période de ponte. Un effet femelle a été aussi significatif pour cinq variables : le poids des œufs, le taux de fécondation, la taille des larves à l'éclosion, le poids final et la résistance au jeûne. Des homogénéités ont été retrouvées entre les œufs et les larves des différentes femelles qui ont pondu à différents moments durant la saison de ponte. Ce fait peut suggérer l'existence d'une organisation précoce, dès l'éclosion, de la qualité des larves chez le brochet qui a engendré deux types de larves ayant des caractéristiques différentes : des larves tardives de grande taille et à croissance rapide et des larves précoces, plus petites mais qui survivent plus longtemps et qui résistent mieux à des conditions trophiques défavorables. Cette particularité pourrait être liée à des aptitudes métaboliques pour ces larves qui éclosent tôt en début du printemps leur permettant de diminuer leurs dépenses énergétiques et de survivre plus longtemps en l'absence d'alimentation adéquate.

Many factors influence larval quality in fish among which are broodstock characteristics, incubation and larval rearing conditions (Huston and De Angelis, 1987). Broodstock characteristics (age, size) and nutrition (food composition, ration) affect the gamete properties, particularly the oocyte, which contains free molecules and hormones like cortisol, insulin-growth factors, RNA transcripts (Gorbman, 1983; Miwa *et al*., 1992; Takagi *et al*., 1994; Brooks *et al*., 1997; McCormick et Nechaev, 2002; Bobe *et al*., 2003). In many fish species, the oocyte composition changes during the spawning season, and influences larval quality at hatch and during subsequent life stages. For example, in thin snook *Centropomus undecimalis* (Bloch, 1792), Yanes-Roca *et al*. (2008) showed that egg quality was higher (high fertilization and hatching rates associated with higher survival rate of larvae) at the beginning of the spawning season because early spawned eggs contained a high concentration of docosahexaenoic acid (DHA). Similarly, Horwood (1990) studied the European plaice *Pleuronectes platessa* (Linnaeus, 1758) and shown that early spawned eggs were larger and contained more yolk reserves compared to eggs spawned later. Moreover, larvae arisen from early spawned eggs were found to resist longer to a food shortage. Kestemont *et al*. (1999) observed for the Eurasian perch *Perca fluviatilis* (Linnaeus, 1758) that eggs spawned later on the spawning season were of poor quality, contained a high concentration of cathepsine L, enzyme which is responsible for the early yolk degradation, low fertilization rate, premature hatch and high mortality of larvae. For this same species, Abi-Ayad (1997) and Migaud (2002) showed that such variation in egg quality during a spawning

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season was responsible for a size difference between newly hatched larvae and a differential growth rate during larval period. Size heterogeneity at early life stages in fish is particularly important to study because it is involved in juvenile fish cohort dynamics that affects the recruitment to the adult stock of a fish population (De Angelis *et al*., 1993). Moreover, initial size heterogeneity is considered to be a key to cannibalism and growth depensation (see Kestemont *et al*., 2003 and references therein) especially for piscivorous species like the northern pike *Esox lucius* where social interactions, aggressive behaviour and cannibalism were reported to occur at early stages (Craig, 1996).

Esox lucius is a common fish in European and North American freshwaters and in coastal areas of the brackish water of the Baltic Sea (Wootton, 1998). Spawning occurs from February to April in southern Europe and from May to June in Northern regions. Eggs are scattered in small clutches among vegetation over a period of approximately 2-5 days where a single female may lay 8,000 to 100,000 eggs, depending on her size and age. The eggs are left unattended and hatch in approximately 120 degree days (Nilsson, 2006).

In this study, we investigate the variations in pike eggs quality and larval morphometry and characteristics during a spawning season. Ecological consequences and significations will be considered to explain the differences observed.

MATERIALS AND METHODS

Fish and experimental facilities

Six egg batches were obtained by stripping and artificial fertilization of oocytes coming from six females (3 females/ spawning time (ST), Tab. I) at two dates during the spawning season: on March, 16 (ST1) and 23 (ST2). The farm stock contained just a few females in spawning condition at the beginning of March and first trial was programmed for 16th March. Three other egg batches were obtained a week after the second trial date (on March 30) but a high mortality was recorded during incubation period (almost 90%) and it was not possible to consider them in our study. It appeared that the spawning season was short due to environmental conditions in the ponds during the year of the study. Broodstock came from two ponds of the Domaine de Lindre, Moselle, France: Voëte pond (females: F1, F2, F3 (ST1) and F1 (ST2); males: M1 to M11) and Lansquenet pond (F2 and F3 (ST2); M12 to M17) (Tab. I). Breeders were fed live preys (forage fish) throughout their life. Ovulation was induced by a single injection of carp pituitary extracts (4 mg kg^{-1} body weight). Males received a 2 mg kg^{-1} dose of the same hormone in order to increase sperm production. Each egg batch was mixed with milt coming from two to four males (Tab. I).

Just after fertilization, each batch of eggs was placed separately in plastic bags with pure oxygen and transported to the laboratory in polystyrene boxes. Each batch of eggs (26 degree-hours post fertilization) was gradually acclimated to the hatchery water temperature (from 13 to 12°C) and then separately transferred into 2L rectangular clays where eggs were displayed on a single layer. Clays were placed on the hatchery tray where water circulates into a closed circuit with a recirculation and an overflow system. During the entire incubation and larval rearing period, water temperature was maintained at 12 ± 0.5°C (optimal for pike egg/larval survival and development, as reported *in* Cooper, 2000; Farrell and Toner, 2003). Dissolved oxygen level was maintained between 8 and 9 mg L^{-1}. Total ammonia and nitrite concentrations in hatchery water were kept below 0.02 and 0.2 mg L^{-1}, respectively. The photoperiod was fixed at 12L/12D and the light intensity at the water surface was 190 lx.

Experimental protocol

During incubation, eggs were checked every day and dead eggs were removed from the clays with a pipette in order to avoid mycosis development. When hatching began, newly hatched larvae were siphoned every day from incubation clays and transferred into clean ones.

Table I. – Pike (*Esox lucius*) broodstock characteristics. F: female; M: male; ST: spawning time.

Spawning time	Females	Size (cm)	Weight (kg)	Oocyte weight (g)	Males
March 16 (ST1)	F1 (ST1)	74.0	3.250	135	M1 (43.0 cm; 0.475 kg) M2 (41.0 cm; 0.425 kg) M3 (60.5 cm; 1.350 kg)
	F2 (ST1)	72.0	2.025	680	M4 (43.0 cm; 0.550 kg) M5 (48.5 cm; 0.650 kg) M6 (45.5 cm; 0.550 kg)
	F3 (ST1)	69.0	2.200	380	M7 (43.0 cm; 0.525 kg) M8 (42.0 cm; 0.475 kg) M9 (60.0 cm; 1.350 kg)
March 23 (ST2)	F1 (ST2)	65.0	1.800	350	M10 (73.0 cm; 1.500 kg) M11 (73.0 cm; 1.500 kg)
	F2 (ST2)	85.0	3.800	1000	M12 (71.0 cm; 2.300 kg) M13 (66.5 cm; 2.250 kg) M14 (64.0cm; 1.900 kg)
	F3 (ST2)	94.5	4.800	1350	M15 (57.0 cm; 1.300 kg) M16 (63.0 cm; 1.900 kg) M17 (63.0 cm; 1.500 kg)

At the sixth day after hatching, when a large quantity of the yolk was absorbed (70-80%), we began the feeding protocol. Larvae received four rations of freshly hatched *Artemia* nauplii (AF and AG strains, INVE, Dendemonde, Belgium) according to a feeding rate fixed at 40% for the first day then decreased by 1% per day (Fiogbé *et al*., 1996) to reach 19% at the end of the experiment (the 21st day post-hatching). For the experiment relative to the resistance to starvation test, sampled larvae were kept without food.

Observations and measurements

Egg quality

In order to assess egg quality, we evaluated four parameters: (1) egg diameter (2) egg weight, (3) fertilization rate and (4) hatching rate.

At reception of the eggs in the laboratory, three samples of about thirteen eggs per spawn were placed on Petri dishes to measure their diameter (mm) under a binocular microscope with a micrometric ocular (Leica Wild M3C) and their weight (mg) under a precision balance (Denver Instrument APX-323) to the nearest 0.0001 g. Then, after 24 hours, fertilization rate was assessed based on the observation of three samples of about thirteen eggs per female. Unfertilized eggs were easily identified to the naked eye due to their white colour.

For the hatching rate calculation, three samples of 100 fertilized eggs per female at the eyed stage (4th day post fertilization) were sampled from the incubators and placed randomly on three clays (100 egg / clay). The hatching rate was determined as the proportion of hatched eggs to total eggs observed at the end of the hatching period.

Larval morphometrics

For each female (egg batch), 90 larvae (30 larvae at each day of hatching, hatching lasted three days) were sampled at hatch and at the 21st day post hatching. They were put into 40 ml glass beakers with 5ml formalin (4%) and at the end of the experiment they were measured for total length (TL) and wet weight using the same material used for egg size and weight measurements.

Resistance tests

Larval resistance to osmotic stress was tested with samples of 90 larvae per female (30 larvae at each day of hatching) that were isolated in glass beakers containing 1L of NaCl solution (2%). Dead larvae were counted after 90 min of exposure.

For the starvation test, three samples of 150 larvae per female (each sample corresponds to each day of hatching) were put into net cages (1.5L) and placed on the tray of the hatchery. Larvae were kept without food and the dead ones were removed and counted every day. The resistance to starvation was expressed as (LP50 = median lethal period) corresponding to the number of days when 50% of larvae were dead.

Larval characteristics

Larval growth was evaluated by computing the specific growth rate in length (*SGRL*) according to the following formula: $SGRL = 100 \times (Ln (L_f) – Ln (L_i)) / day$, where L_f: total length measured at the 21st day of the experiment and L_i: total length measured at hatch.

For the survival rate (*Sr*) estimation, three samples of 150 larvae per egg batch, that correspond to larvae hatched at each day of hatching, were put in individual clays, fed according to the feeding plan explained above and dead larvae were removed and counted every day. The survival rate was calculated according to the formula: $Sr = N_f \times 100 / N_i$ where N_f: final number of larvae surviving at the 21st day and N_i: initial number of larvae

Statistical analysis

Two factors ANOVA: spawning time ST (DF = 1) and female (nested under spawning time, DF = 4) were performed on data characterizing eggs and larvae using a GLM procedure (SAS, Littel *et al*., 1996). The normality of the results was tested by a Univariate procedure and Bonferroni and Tukey tests (HSD) were considered to compare the adjusted means (Ls means).

For all statistical analysis, the coefficient of variation of the root mean square error (CV RMSE) was indicated. The minimum level of significance was set at $p < 0.05$.

RESULTS

The first larva appeared at the 10th day of incubation. Hatching lasted three days (March, 26, 27 and 28 for eggs spawned on March, 16 and April, 3, 4 and 5 for eggs spawned on March, 23).

The spawning time (ST) effect was significant for ten variables: the egg weight (We), the fertilization rate, (FR), the hatching (HR), the initial length and weight of larvae (TL_i, W_i), the specific growth rate in length (SGRL), the final length and weight (TL_f, W_f), the resistance to starvation (LP50) and the survival rate (Sr). The female effect (F) was significant for five parameters: the egg weight, the fertilization rate, the initial larval size, the final larval weight and the resistance of larvae to starvation.

Egg quality

Neither spawning time nor female was found to affect the egg diameter in our experiment. Early and late spawned eggs presented similar diameter (3.16 mm for egg spawned on March, 16 *vs* 3.07 mm for egg spawned on March, 23; $p > 0.05$). However, egg weight was significantly ($p = 0.01$)

Table II. - Experimental results (Ls means). CVRMSE: Coefficient of Variation of the Root Mean Squared Error; FR: fertilization rate of eggs; HR: hatching rate; LP50: median lethal period; SGRL: specific growth rate in length; SR: survival rate; TL: total length; W: weight; i: initial (at hatch), f: final (at day 21 post-hatching, end of the experiment).

Spawning time	March 16	March 23	CVRMSE
FR (%)	88.30	71.13	9.1%
HR (%)	97.12	80.67	9.8%
TL_i (mm)	8,87	9.24	0.7%
W_i (mg)	8.45	10.53	4.1%
SGRL (%)	3.79	4.13	2.5%
SR (%)	71.99	59.11	6.4%
LP50 (days)	21.00	19.11	1.4%
TL_f (mm)	19.66	22.01	2.1%
W_f (mg)	47.17	72.54	2.7%

higher for late spawned eggs compared to early spawned ones (Tab. II). Depending on the female, the difference in egg weight was more or less important and sometimes egg weight was similar for females that spawned at different dates (Fig. 1A).

On the other hand, fertilization and hatching rates were significantly influenced by the spawning time. Early spawned eggs showed lower fertilization rate but higher hatching rate, compared to the late spawned ones (Tab. II). For fertilization rate, there was also a significant female effect (Fig. 1B) where we noted that the highest difference in fertilization rate (43%) was recorded for eggs from the females F3 (ST1) and F3 (ST2). We observed also that the fertilization rate of eggs from F1 (ST1) was similar to that of eggs from all females of the late spawning time [F1, F2, and F3 (ST2)].

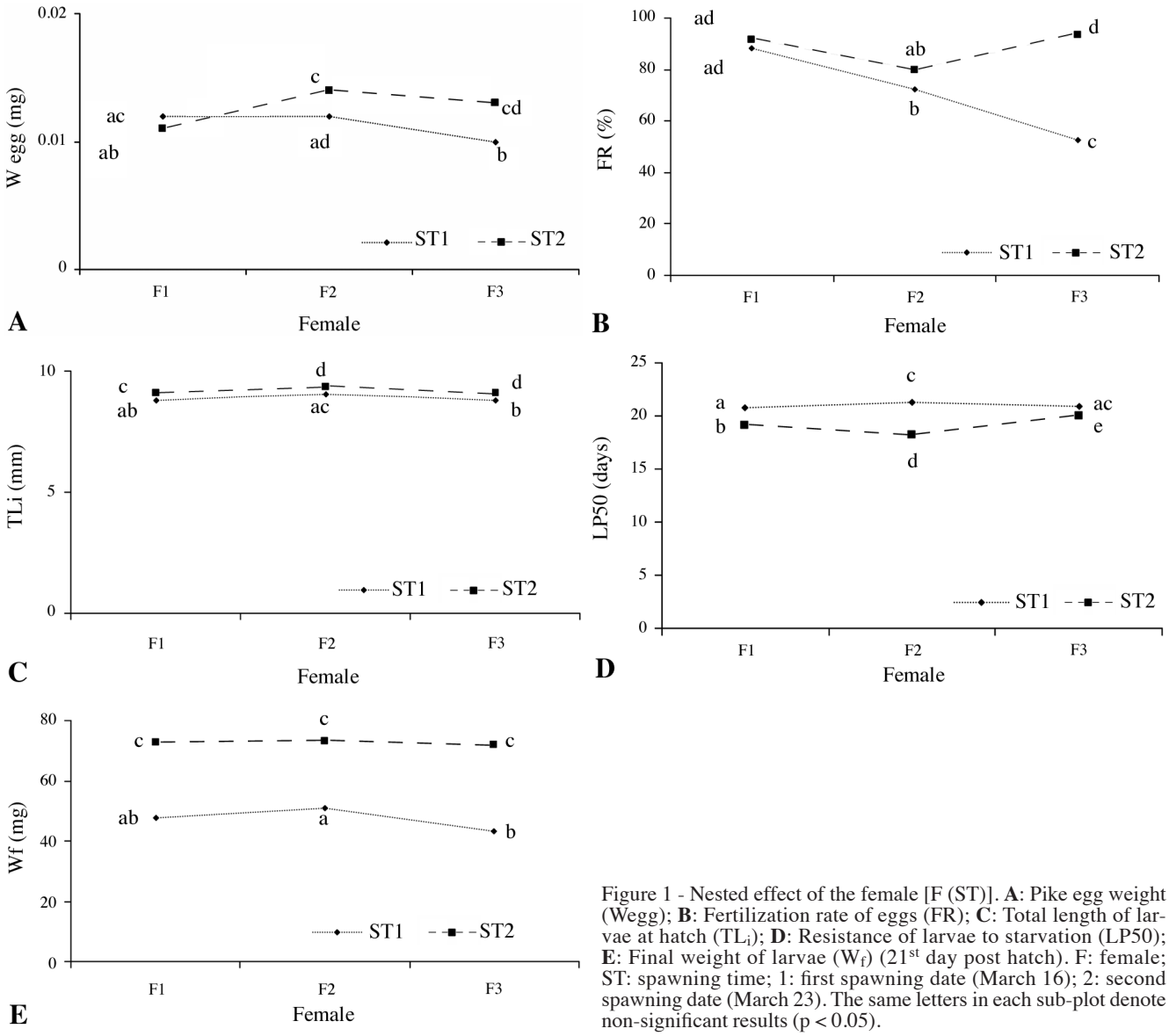

Figure 1 - Nested effect of the female [F (ST)]. **A**: Pike egg weight (Wegg); **B**: Fertilization rate of eggs (FR); **C**: Total length of larvae at hatch (TL_i); **D**: Resistance of larvae to starvation (LP50); **E**: Final weight of larvae (W_f) (21st day post hatch). F: female; ST: spawning time; 1: first spawning date (March 16); 2: second spawning date (March 23). The same letters in each sub-plot denote non-significant results ($p < 0.05$).

Larval quality

Initial size and weight

Pike larval size at hatching (TL_i) was significantly influenced by both ST ($p < 0.0001$) and F ($p = 0.0001$) while the initial weight (W_i) was influenced only by the spawning time. Globally, larvae hatched from eggs spawned on March 23 were significantly larger and heavier than those spawned earlier (Tab. II). For TL_i, there was a significant nested female effect presented in figure 1C, where we remark a size homogeneity between larvae from females within a same spawning time [females F2(ST2) and F3(ST2)] and also between spawning times [females F2(ST1) and F1 (ST2)].

Resistance tests

Starvation test revealed that larvae hatched from eggs spawned on March 16 resisted longer to the absence of food compared to those spawned later (Tab. II). This difference was the highest (14.5%) between the females F2 (ST1) and F2 (ST2) (Fig. 1D). On the other hand, neither spawning time nor female influenced the resistance to osmotic stress for pike larvae. All larvae survived until 90 min of exposure to saline water.

Growth and survival rates

Specific growth rate and survival rate for pike larvae computed at the end of the experiment were significantly influenced by the spawning time ($p < 0.0001$) and not by the female. Spawning time influenced differently these two quality indicators. We observed an increase in the SGRL and a decrease in the survival rate when the spawning period progressed. This implies that larvae hatched earlier on the reproduction period (March 16) grew slower than larvae hatched later (March 23) but survived longer (Tab. II).

Final size and weight

At the end of the experiment (21st day), size and weight measurements showed that larvae hatched from eggs spawned on March 23 were 10% larger and 36% heavier ($p < 0.0001$) than larvae spawned earlier (Tab. II). Final weights were similar for larvae coming from females F1, F2 and F3 (ST2) but differed little for larvae from the females that spawned on March 16 (Fig 1E).

DISCUSSION

Fish reproduction occurs according to a temporal organisation and spawning season for each species takes place when favourable conditions are present like temperature, hydrology, access to spawning areas, survival of embryos and larvae (Bruslé and Quignard, 2004). Protracted spawning season is common for many fish species and affects oocyte composition *e.g.* lipids (Yanes-Roca *et al.*, 2008) and larval and juvenile development *e.g.* growth and survival (Abi-Ayad, 1997; Migaud, 2002; Chalde *et al.,* 2014).

Spawning time effect

Our study revealed that pike eggs spawned on March 16 were 15% lighter than eggs spawned later and they presented lower fertilization rate (-19%) but higher hatching rate (+16%). Larvae hatched from early spawned eggs presented smaller sizes at hatch (-4% TL_i, -19% W_i) and at the end of larval period (-10% TL_f, -36% W_f), lower growth rate (-8%) but higher survival (+17%) and resistance to starvation (+9%) compared to larvae hatched later. Egg size and resistance to osmotic stress were not affected by spawning time; they remained almost constant during the spawning season. The mean egg diameter computed for the two spawning times was 3.11 mm, which agrees with earlier data on pike egg size cited in the literature (1.5 to 3.1 mm: Frost and Kipling, 1967; Chauveheid and Billard, 1983; Farrell *et al.*, 1996). On the other hand, egg weight was significantly higher for eggs spawned on March 23 compared to eggs spawned earlier (Tab. II) that can imply a greater quantity of yolk and nutrients in late spawned eggs. These results are in accordance with those reported by Murry *et al.* (2008), where pike egg diameter did not differ with spawning season but dry weight was greater in late spawners.

Fertilization rates for eggs from the two spawning periods were high except for the female F3 (ST1) where it was 52% only. This low value was responsible for the decrease of the total fertilization rate computed for eggs of the spawning time ST1 (March 16) and could explain the significant difference in fertilisation rate observed between the two spawning times (88.3% for ST2 *vs* 71.13 for ST1; Tab. II). Provided that there was a homogeneity in females characteristics for this spawning time ST1 and a little difference for the others measured parameters between larvae of these females. There was probably a technical problem that occurred when realising the artificial fertilization for this female and led to the low fertilization rate obtained in our experiment.

Hatching rate, resistance to starvation and survival rate were significantly higher for eggs spawned earlier on the spawning season compared to eggs spawned later (Tab. I). These findings agree with previous studies where early spawned eggs presented higher hatching rates (Murry *et al.*, 2008; Yanes-Roca, 2008; Chalde *et al.*, 2014) compared to late spawned ones and early hatched larvae showed higher resistance to starvation (Horwood, 1990) and higher survival rate (Yanes-Roca, 2008; Chalde *et al.*, 2014) compared to late hatched ones. Given that, the success of the embryonic development and further survival of larvae depends strongly on egg yolk reserves quality (Kjorsvik *et al.* 1990; Bromage & Roberts, 1995). We can thus conclude that eggs spawned at the beginning of the spawning season presented a better quality compared to those spawned later. This higher quality,

independent of egg weight, may be related to a high concentration on early spawned oocytes of some molecules, particularly DHA as was reported by Yanes-Roca (2008) for the thin snook.

In fact, Satoh *et al*. (2005) showed that DHA improved survival and resistance to starvation in larval brown sole (*Pleuronectes herzensteini* Jordan & Snyder, 1901), which confirms ours findings. This capacity to survive in the absence of food may be related to a physiological particularity for these larvae that allow them to reduce their energetic demands (respiration, swimming, metabolism…), decreasing the yolk absorption speed. This ability characterises small size individuals as reported by Giguere *et al*. (1988) and Nelson and Wilkins (1994), which corresponds to larvae hatched from early spawned eggs in our study.

The decrease in larval survival when spawning period progressed agrees with previous conclusions about a drop in the reproduction performance and a poor quality of late spawned eggs (Kjorsvik *et al*., 1990; Treasurer and Ford, 2010; Castets *et al*., 2012). This result can be explained by a possible overripening and by a precocious protein degradation of oocytes when kept within the female abdominal cavity more than necessary. This overripening phenomenon was reported by Kestemont *et al*. (1999) in perch and the enzyme responsible of it is the cathepsine L. According to Aegerter and Jalabert (2004) and Aegerter *et al*. (2005), the cathepsine L causes a decrease in larval survival rate.

Our study revealed that larvae hatched from eggs spawned on March 23 showed better growth rates and higher sizes at hatch and after 21 days of rearing compared to larvae hatched earlier. This finding agrees with Murry *et al*. (2008) observations, where late season larvae from late spawned eggs were markedly larger at hatch and at swim up stage compared to larvae from early spawned eggs. Enhanced growth is generally obtained by increased efficiency to convert yolk into tissue and/or a better success to switch from endogenous to exogenous feeding. Increasing the efficiency of yolk use at early stages is possible if the cost of protein synthesis is reduced or when there is a reallocation of energy from maintenance functions to growth process (Wieser *et al*., 1988; Pannevis and Houlihan 1992). Thus, larvae hatched from late spawned eggs may have this particular metabolic plasticity allowing achieving a higher growth.

Female effect

In our study, the female effect was significant for five variables: egg weight, fertilization rate, initial size, final weight and resistance to starvation.

For the egg weight, our results showed that the heaviest eggs were obtained from late spawning females F2 and F3 (ST2) (Fig. 1A). Theses females were the largest among the six females considered in our experiment (Tab. I) and their offspring presented significantly higher sizes compared to the offspring of the other females (Fig. 1C). This result confirms previous correlations established between female size on one hand, and egg and offspring sizes on the other hand: for examples, Ojanguren *et al*. (1996) in brown trout *Salmo trutta* L. and Hislop (1988) for haddock *Melanogramus aiglefinus* (Linnaeus, 1758). Moreover, the egg weight of the late spawned female F1 (ST2) was similar to that of all early spawned ones ($p < 0.05$), which could be explained by the morphometric characteristics (size) of this female F1 (ST2) that were closer to early spawned females than to the late spawned ones.

For the other variables, the female effect was weak and did not reflect the initial differences in egg weight. This implies that other factors than female size may influence larval size and characteristics during a spawning season. This relationship is complex and may depend on other factors like female condition, prey availability and population structure.

Ecological significance

Our results showed that according to the timing of spawning during a reproduction season, there are two different "qualities" of larvae for the northern pike. Early season individuals presented small size at hatch, slow growth but high survival and resistance to starvation. The occurrence of such characteristics would match with instable environmental conditions, particularly with food availability. In this case, larvae can reduce their energetic demands in order to use efficiently remained yolk until the environmental conditions became favourable. These environmental conditions correspond to the early spring season (reproduction season for the northern pike) where temperature fluctuations are frequent and conditioning prey availability (zooplankton) unpredictable.

On the other hand, late season individuals showed larger sizes at hatch and accelerated growth. Increased size is known to be advantageous since larger larvae are characterised by a better ability to find and capture preys, to endure period of low food abundance and to avoid predation (Heyer *et al*., 2001; Ouellet *et al*., 2001; Browman *et al*., 2003). Theses capacities are observed in natural conditions and they may be not well-expressed at laboratory conditions because predators are absent and food is available. Enhanced growth of larvae hatched at late season may be considered as a reproductive adaptation to maximise the size of the fingerlings in situation when the growing season is short (Murry *et al*., 2008).

Finally, from an evolutionary perspective, the production of offspring of variable size during a reproduction season (early season *vs* late season) may be considered as bet-hedging strategy in a variable environment of temperature, food availability, and predator risk (Laurel and Blood, 2011). The occurrence of size heterogeneity in larval stage may be also regarded as a "strategy", which favours the development of

cannibalism as normal behaviour and diet for pike. It was reported also to occur at early life stages (Hecht and Appelbaum, 1988; Katavic *et al*., 1989).

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